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NEW *GOMPHONEMA* (BACILLARIOPHYCEAE) SPECIES  
FROM MADAGASCAR

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Nine new species of diatoms (Bacillariophyceae) of the genus *Gomphonema* Ehrenberg are described from the island-continent of Madagascar. A number of the Madagascar taxa are astigmatate, an unusual finding, since a large fraction of diatoms within the genus *Gomphonema* possess a central stigma. The astigmatate taxa also possess the feature of an axial plate, solid thickenings of silica extending perpendicular from the axial area. These *Gomphonema* are unique because they are the only species within the genus known to possess such structures. Based on examination in the SEM, we suggest that the axial plates of the astigmatate *Gomphonema* may not be homologous to the axial plates of other gomphonemoid diatoms (*Gomphoneis herculeana* group). We compare valve morphology of astigmatate *Gomphonema* from Madagascar with that of astigmatate *Gomphonema* of other regions. This comparison provides evidence that *Gomphonema* of Madagascar, South America, Africa and Asia are each limited to narrow biogeographic ranges. The rich diatom flora of Madagascar, especially of astigmatate gomphonemoid forms with axial plates, forms a distinct endemic lineage.

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Although over 1000 taxa of *Gomphonema* have been described [Van Landingham (1971) lists just over 940 published up to 1960], and less than 5% of them have been documented with SEM (Gaul et al. 1993), the genus has been shown to be heterogeneous with regard to valve ultrastructure. Recent work by Passy et al. (1997), Kociolek and Stoermer (1991a, 1991b, 1993) and Kociolek and Kingston (submitted) have shown variation in striae construction, stigma position, size and morphology, raphe organization and apical pore field composition and position. Researchers continue to document variation in well-known species, as well as continue

to uncover new taxa in geographic regions thought to be familiar in terms of the diatom flora (Lange-Bertalot 1993; Lange-Bertalot and Metzeltin 1996), as well as in more exotic regions (e.g., Passy et al. 1997). In this report we describe valve morphology and variability in nine new *Gomphonema* species from the island-continent of Madagascar.

MATERIALS AND METHODS

A collection of material from Madagascar was obtained from the Laboratoire de Cryptogamie, Museum National d'Histoire Naturelle (MNHN,

Paris) with the following locality information, "Mission R. Heim, Cascade Ankitso 24/9/34." Material was also obtained from the West and West Collection (L666) of the British Museum of Natural History (BMNH). Material from the collections was boiled in  $\text{HNO}_3$ , then washed by repeated rinsing and settling in distilled water. The cleaned material was air dried onto cover-glasses and mounted on slides using Naphrax or Hyrax. Material was accessioned in to the Diatom Collection at CAS (Cascade Ankitso sample #615809, West and West collection #615816). Slides obtained on loan from the Manguin Collection (MNHN) were also examined (AD 8499–8500, 8533–8535, 8608–8609, 8643–8650, 8655–8659, 8665–8676, 8715–8716). These slides were made from material of lacustrine fossil deposits of the Ankaratra Mountains of the Ranomafana region of Madagascar and are the type localities of *Gomphonema brasiliense* var. *demerarae* fo. *obtusum* Manguin (1949a), *Gomphonema brasiliense* var. *rhombiformis* Manguin (1952), and *Gomphonema brasiliense* var. *subclavatum* Manguin (1952). Light microscope observations were made with a Leitz DMRB (1.4 NA). Scanning electron microscope observations were made on material air dried onto cover-glasses and air dried onto aluminum stubs. The stubs were sputter-coated with approximately 20 nm Au and viewed on a Hitachi H-520 SEM at operating voltages of 15–25 kV.

## RESULTS

### *Gomphonema* Ehrenberg 1832

*Gomphonema perinsignis* Spaulding & Kociolek, sp. nov.  
(Figs. 1–6, 43–48)

*DESCRIPTIO*. — *Valvae trullatae, capitulo-polo rotundato anguste, basi-polo rotundato. Longitudo 35–63 μm. Latitudo 8–11 μm. Area axialis lanceolata late. Stigma carens. Raphe lateralis undulata. Extrema raphium extra proximalia dilata. Extrema raphium interna proximalia deflexa lateraliter. Lineae longitudinalis prope margines in latere alteruto areis axialis. Striae ad centrum (12–14/10 μm) parallellae, ad capitulum-polum (12–16/10 μm) et basim-polum (12–14/10 μm) radiatae. Area porellibus*

*apicalis bilobata distincta et basim-polum. Pseudoseptum distinctum.*

*DESCRIPTION*. — Valves trullate with narrowly-rounded headpole and rounded footpole. Length 35–63 μm. Breadth 8–11 μm. Axial area broadly lanceolate. Stigma lacking. Raphe lateral, undulate. External proximal raphe ends dilated, internal proximal raphe ends deflected laterally. Striae crossed by longitudinal lines near the margin on both sides of the axial area. Striae parallel at the center (12–14/10 μm), radiate at the headpole (12–16/10 μm) and footpole (12–14/10 μm). A bilobed apical pore field is evident at the footpole. Pseudosepta distinct.

*HOLOTYPE*. — CAS 219037 (Figs. 3, 4).

*TYPE LOCALITY*. — Surface of wet rocks, Cascade Ankitso, Madagascar.

In the SEM, puncta are lineolate externally (Figs. 43, 44) and extend over the valve margin and onto mantle. Puncta at headpole lineolate (Fig. 45). Near the axial area, striae appear as dark bands midway between the margin and axial area (Fig. 43). The dark bands are formed by foramina that are occluded by an axial plate (as in *G. evanescens*, Fig. 52). Externally, proximal raphe ends are distinctly bulbous (Fig. 43), and raphe narrow and indistinct. At the headpole, the raphe has a slight bend, and is slightly offset from the apical axis at the valve margin (Fig. 45). On some valves, a small broad spine is found at the headpole valve margin (Fig. 44). At the footpole, the raphe has a slight hook near the valve margin, and extends over mantle in a straight line (Fig. 47). Apical pore field present, composed of simple porellis (Figs. 46, 47). Internally, pseudosepta and helictoglossae are distinct (as in *G. evanescens*, Fig. 53). Central nodule broad and rectangular, unilaterally expanded (as in *G. evanescens*, Fig. 52).

*COMMENTS*. — This species differs from other Madagascar *Gomphonemas* in shape and possesses an axial plate and marginal lamina. Although the structure of the axial plate under SEM appears similar to that of diatoms in the *Gomphoneis herculeana* group (Kociolek and Stoermer 1988, 1993), with LM the longitudinal lines are unique in appearance. The longitudinal line (edge of axial plate) is evident in LM as striae that "disappear," or are reminiscent of ghost striae. These structures are evident when specimens are optically dissected from high to low level of focus. Such an appearance in LM con-

trasts with the characteristic longitudinal lines of the *Gomphoneis herculeana* group of gomphonemoid diatoms. *Gomphonema perinsignis* is the most abundant member of the genus within the collections examined and the largest of 6 closely related astigmatate species described here. This taxon is similar in valve shape to the original illustrations of *G. brasiliense* var. *demerarae* fo. *obtusa* Manguin (1949a:115, fig. 70a, b), described from fossil material from the Ankaratra region of Madagascar. Slides from the type locality (Ankaratra Region, Sambaina-Mandrosohasina Basin, Section Mandrosohasina) of the Manguin Collection (AD 8608, 8609) were examined, however no specimens fitting Manguin's description of *G. brasiliense* var. *demerarae* fo. *obtusa* were observed. *Gomphonema perinsignis* and *G. brasiliense* var. *demerarae* fo. *obtusa* overlap in length (36–63  $\mu\text{m}$  vs. 23–51  $\mu\text{m}$ ) and breadth (8–11  $\mu\text{m}$  vs. 5–8.5  $\mu\text{m}$ ) respectively. The two are distinguished by striae count (12–16/10  $\mu\text{m}$  vs. 10–11/10  $\mu\text{m}$ ). Further collections from Madagascar, however, may show them to be synonymous. Manguin (1952) described two additional astigmatate gomphonemoid taxa from Madagascar (*G. brasiliense* var. *rhombiformis* and *G. brasiliense* var. *subclavata*). Manguin's illustrations (1952:35, figs. 76, 77) indicate a wide axial area, a feature in common with *G. perinsignis* and the other taxa newly described herein. Type slides from the Manguin Collection were carefully examined (Antsirabe, Niv. 20 m slides: AD 8499–8500, 8533–8535, 8643–8650, 8655–8659, 8665–8676, 8715–8716) and four astigmatate gomphonemoid specimens (see specimen illustrated in Fig. 3) were found in four slides (AD 8666, 8648, 8650, 8655). These four specimens fit the size range of *G. perinsignis*, which is significantly larger than the Manguin varieties (Table 1). In summary, we have been unable to locate specimens in the Manguin Collection conforming to the descriptions of any of the three astigmatate diatom taxa previously proposed.

***Gomphonema madagascarenis*** Spaulding & Kociolek, sp. nov.  
(Figs. 7–9)

*DESCRIPTIO.* — *Valvae ovatae, capitulo-polo et basi-polo rotundato. Longitudo 35–37  $\mu\text{m}$ . Latitudo 7.5–8.5  $\mu\text{m}$ . Area axialis lanceolata*

*late. Stigma carens. Raphe lateralis undulata. Extrema raphium extra proximalia dilata. Extrema raphium interna proximalia deflexa lateraliter. Striae ad centrum (12–13/10  $\mu\text{m}$ ) parallelae, ad capitulum-polum (14–15/10  $\mu\text{m}$ ) et basim-polum (13/10  $\mu\text{m}$ ) radiatae. Area porellibus apicalis bilobata distincta et basim-polum. Pseudoseptum distinctum.*

*DESCRIPTION.* — Valves ovate with headpole and footpole rounded. Length 35–37  $\mu\text{m}$ . Breadth 7.5–8.5  $\mu\text{m}$ . Axial area broadly lanceolate. Stigma lacking. Raphe lateral, undulate. External proximal raphe ends dilated, internal proximal raphe ends deflected laterally. Striae parallel at the center (12–13/10  $\mu\text{m}$ ), radiate at the headpole (14–15/10  $\mu\text{m}$ ) and footpole (13/10  $\mu\text{m}$ ). A bilobed apical pore field is evident at the footpole. Pseudosepta distinct.

*HOLOTYPE.* — CAS 219036 (Fig. 8).

*TYPE LOCALITY.* — Surface of wet rocks, Cascade Ankitso, Madagascar.

*COMMENTS.* — *Gomphonema madagascarenis* differs from *G. perinsignis* in shape; it is broadly ovate in outline, in contrast to the trullate valves of *G. perinsignis*. The valve shapes of *G. madagascarenis* and *G. perinsignis* are distinct and do not overlap with changes in valve length and width in either size diminution series. Like *G. perinsignis*, *G. madagascarenis* possesses a characteristic axial plate, evident in the LM as striae that form the image of longitudinal lines.

***Gomphonema evanescens*** Spaulding & Kociolek, sp. nov.  
(Figs. 10–12, 49–55)

*DESCRIPTIO.* — *Valvae cuneatae lineares, capitulo-polo et basi-polo rotundato. Longitudo 34–36  $\mu\text{m}$ . Latitudo 6–7  $\mu\text{m}$ . Area axialis lanceolata. Stigma carens. Raphe lateralis undulata. Extrema raphium extra proximalia dilata. Extrema raphium interna proximalia deflexa lateraliter. Area porellibus apicalis bilobata distincta et basim-polum. Striae ad centrum (12–13/10  $\mu\text{m}$ ) parallelae, ad capitulum-polum (13–14/10  $\mu\text{m}$ ) et basim-polum (12/10  $\mu\text{m}$ ) radiatae. Pseudoseptum distinctum.*

*DESCRIPTION.* — Valves cuneate, linear, with headpole rounded, footpole narrowly rounded. Length 34–36  $\mu\text{m}$ . Breadth 6–7  $\mu\text{m}$ . Axial area lanceolate. Stigma lacking. Raphe lateral, undulate. External proximal raphe ends dilated. Inter-

TABLE 1. Summary of the valve morphology of *Gomphonema* species.

Taxon	Length ( $\mu\text{m}$ )	Width ( $\mu\text{m}$ )	Stigma	Shape
<i>G. perinsignis</i>	36–63	8–11	absent	trullate, with narrowly rounded headpole and footpole
<i>G. madagascarensis</i>	35–37	7.5–8	absent	ovate, with rounded headpole and footpole
<i>G. evansescens</i>	34–36	6–7	absent	cuneate, linear, with rounded headpole and narrowly rounded footpole
<i>G. westii</i>	24–30	5.5–6	absent	cuneate, broadly rounded headpole and narrowly rounded footpole
<i>G. peracutum</i>	17.5–22	3	absent	linear, headpole rounded, footpole narrowly rounded
<i>G. quadratarea</i>	16–21	3.2–3.5	absent	linear, cuneate with headpole rounded, footpole acute
<i>G. eurycephalus</i>	26–49	7–9	present	cuneate, linear, with broadly rounded headpole and rounded footpole
<i>G. stigmatellum</i>	18–27	3.5–5	present	linear to lanceolate-cuneate, headpole narrow to rounded, footpole narrow
<i>G. pulvillum</i>	17–36	6	present	club-shaped, linear to broadly lanceolate, headpole produced and broadly rounded, footpole produced, rounded
<i>G. brasiliense</i> var. <i>demerarae</i> fo. <i>obusa</i>	23–51	5–8.5	absent	Manguin (1949:102, fig. 70a, b)
<i>G. brasiliense</i> var. <i>rhombiformis</i>	20	4	absent	Manguin (1952:36, fig. 76)
<i>G. brasiliense</i> var. <i>subclavata</i>	24	3.5	absent	Manguin (1952:36, fig. 77)

nal proximal raphe ends laterally deflected. At the footpole is a distinct apical pore field, composed of two lobes. Striae crossed by longitudinal lines near the margin on both sides of the axial area. Striae parallel at the center (12–13/10  $\mu\text{m}$ ), radiate at the headpole (13–14/10  $\mu\text{m}$ ) and footpole (12/10  $\mu\text{m}$ ). Pseudosepta distinct.

HOLOTYPE. — CAS 219036 (Fig. 11).

TYPE LOCALITY. — Surface of wet rocks, Cascade Ankitso, Madagascar.

In the SEM, puncta are lineolate externally and extend over valve margin and onto mantle (Figs.

49–51). Puncta at headpole lineolate (Fig. 55). Externally, proximal raphe ends are distinctly expanded (Fig. 51). Raphe narrow (Figs. 54, 55). At the headpole, the raphe has slight bend, and is slightly offset from the apical axis at the valve margin (Fig. 55). At the footpole, the raphe has a slight hook near the valve margin, raphe extends over mantle in a straight line (Fig. 54). Pore field present at the footpole, composed of simple porelli (Fig. 54). Internally, pseudosepta and helictoglossae distinct (Figs. 52, 53). Axial plate and marginal lamina present (Figs. 52, 53). Cen-

TABLE I. (continued)

Axial area	External proximal raphe	Internal proximal raphe	Striae in 10 $\mu$ m
broadly lanceolate	dilated	laterally deflected	C 12–14 parallel H 12–16 radiate F 12–14 radiate
broadly lanceolate	dilated	laterally deflected	C 12–13 parallel H 14–15 radiate F 13 radiate
lanceolate	dilated	laterally deflected	C 12–13 parallel H 13–14 radiate F 12 radiate
narrow at poles, expanded into an ovoid central area	dilated	laterally deflected	C 10–12 parallel H 13–14 slightly radiate F 12–13 radiate
narrow at poles, expanded into an ovoid central area	prominently dilated	laterally deflected	C 13 parallel H 15–16 slightly radiate F 13–16 strongly radiate
narrow, linear with rectangular to slightly ovoid central area	slightly dilated	slightly laterally deflected	C 14 parallel H 16–18 parallel to slightly radiate F 14–16 slightly radiate
narrow, with small ovoid asymmetric central area	slightly dilated	laterally deflected toward stigmas	C 8–10 slightly radiate H 12 parallel to radiate F 10–12 radiate
narrow at apices, expanded into broadly rounded central area	dilated	hooked toward stigma	C 12–14 parallel H 14–16 slightly radiate F 13 radiate
axial area narrow at poles, lanceolate	slightly dilated, curved toward stigma	laterally deflected	C 10–12 slightly radiate H 12 slightly radiate to parallel F 13–14 strongly radiate 10–11  12–13  18

tral nodule broad, slightly constricted, unilaterally expanded (Fig. 52). Proximal raphe ends not visible in the valve interior.

COMMENTS. — *Gomphonema evanescens* has the most linear-elongate valves of the astigmatate species complex from Madagascar. This taxon differs from *G. perinsignis* and *G. madagascarensis* in shape of the central area; the central area is more narrow in this taxon. Like the other astigmatate taxa, *G. evanescens* possesses an axial plate, evident in the LM as striae that form the image of longitudinal lines.

***Gomphonema eurycephalus*** Spaulding & Kociolek, sp. nov.  
(Figs. 13–18, 69–75)

DESCRIPTION. — *Valvae cuneatae lineares, capitulo-polo late rotundato, basi-polo rotundato. Longitudo 26–49  $\mu$ m. Latitudo 7–9  $\mu$ m. Area axialis angusta. Area centralis parva ovoidea asymmetrica stigmatate singulari. Raphe recta ad dilute undulata lateralis. Extrema raphium extra proximalia dilata. Extrema raphium interna proximalia deflexa versus*

*stigma. Area porellibus apicalis bilobata distincta. Striae punctis in 2 serie, ad centrum (8–10/10  $\mu\text{m}$ ) dilute radiatae, ad capitulum-polum (12/10  $\mu\text{m}$ ) parallelae ad radiatae, basim-polum (10–12/10  $\mu\text{m}$ ) radiatae. Pseudosepta distincta ad polos.*

**DESCRIPTION.** — Valves cuneate, linear, with broadly rounded headpole and rounded footpole. Length 26–49  $\mu\text{m}$ . Breadth 7–9  $\mu\text{m}$ . Axial area narrow, producing a small, oval asymmetric central area. A single large stigma is positioned in the middle of the central area. Raphe straight to slightly undulate, lateral. External proximal raphe ends dilated slightly. Internal proximal raphe ends deflected towards the stigma. Apical pore fields distinct. Striae composed of double rows of puncta, slightly radiate about the center (8–10/10  $\mu\text{m}$ ), parallel to radiate at the headpole (12/10  $\mu\text{m}$ ), radiate at the footpole (10–12/10  $\mu\text{m}$ ). Pseudosepta are distinct at both poles.

**HOLOTYPE.** — CAS 219037 (Fig. 14).

**TYPE LOCALITY.** — Surface of wet rocks, Cascade Ankitso, Madagascar.

In the SEM, striae are doubly punctate, and puncta circular to oval in shape and arranged in alternating rows (Fig. 70). Striae extend over valve mantle (Figs. 69, 70), including at the headpole (Fig. 71). Pore field present at the footpole composed of circular porelli, bisected by the raphe (Fig. 75). Stigma located centrally, with circular external expression (Fig. 70), while internal expression is elongated at the central nodule (Fig. 72). Internally, proximal raphe ends are deflected laterally (Fig. 72) and puncta located within wide foramina. Helictoglossae present at both poles (Figs. 73, 74). Pseudosepta present at footpole, reduced at headpole. Valves were observed to possess two copulae (Fig. 69).

**COMMENTS.** — *Gomphonema eurycephalus* is distinctly doubly punctate and notable for the central position of the stigma, close to the proximal raphe ends. It appears to be closely related to *G. latistigmata* Passy et al. and *G. chohnokyi* Passy et al. of southern Africa (Passy et al. 1997). Each of these taxa have alternating doubly punctate striae, possess a prominent stigma close to the proximal raphe ends, and are somewhat similar in valve outline. In contrast to the South African taxa, *G. eurycephalus* lacks areolae with external vela and possesses an ovoid central area. It is also distinct from *G. aequatoriale* Hustedt, a stigmatate taxon described from Zaire. *Gom-*

*phonema aequatoriale* Hustedt is larger (50–100  $\mu\text{m}$  in length), singly punctate, the central area is less oval, and the stigma is not as centrally positioned compared to *G. eurycephalus*.

**Gomphonema pulvillum** Spaulding & Kociolek, sp. nov.  
(Figs. 19–24)

**DESCRIPTION.** — *Valvae cuneatae lineares ad late lanceolatae, capitulo-polo producto et late rotundato, basi-polo producto rotundato praeter specimina parva. Longitudo 17–36  $\mu\text{m}$ . Latitudo 6  $\mu\text{m}$ . Area axialis lanceolata ad polos angustis. Stigma 1. Raphe undulata lateralis. Extrema raphium extra proximalia dilata deflexa versus stigma. Extrema raphium interna proximalia deflexa lateraliter. Area porellibus apicalis bilobata praesens. Striae latae, ad centrum (10–12/10  $\mu\text{m}$ ) dilute radiatae dispositae magis late, ad capitulum-polum (12/10  $\mu\text{m}$ ) parallelae ad dilute radiatae, ad basim-polum (13–14/10  $\mu\text{m}$ ) valde radiatae. Pseudosepta distincta in valvis grandibus.*

**DESCRIPTION.** — Valves club-shaped, linear to broadly lanceolate, headpole produced and broadly rounded. Footpole produced, rounded except in smaller specimens. Length 17–36  $\mu\text{m}$ . Breadth 6  $\mu\text{m}$ . Axial area lanceolate, narrow at poles. A single stigma is present. Raphe lateral, undulate, with external proximal raphe ends dilated slightly and curved towards stigma, internal proximal raphe ends laterally deflected. Apical pore field present. Striae broad, slightly radiate and more widely spaced at the valve center (10–12/10  $\mu\text{m}$ ), slightly radiate and becoming parallel at the headpole (12/10  $\mu\text{m}$ ), strongly radiate at the footpole (13–14/10  $\mu\text{m}$ ). Pseudosepta evident in larger valves.

**HOLOTYPE.** — CAS 219036 (Fig. 19).

**TYPE LOCALITY.** — Surface of wet rocks, Cascade Ankitso, Madagascar.

**COMMENTS.** — Superficially, this taxon is similar to *Gomphonema biceps* Meister, a diatom described from the Canton River in China (Meister 1934). *Gomphonema biceps* differs from *G. pulvillum* by pronounced capitate headpole and footpole. The footpole of *G. pulvillum* is rounded, but more nearly acute. Further, the striae of *G. biceps* are more radiate in the center of the valve than in *G. pulvillum*.

**Gomphonema stigmatellum** Spaulding & Kociolek, sp. nov.  
(Figs. 25–28)

*DESCRPTIO.* — *Valvae lineares ad lanceolatae-cuneatae, capitulo-polo angusto ad rotundato, basi-polo angusto. Longitudo 18–29 μm. Latitudo 3.5–5 μm. Area axialis sub apice angusta expansa in aream centralem late ovoideam. Stigma 1. Raphe lateralis undulata. Extrema raphium extra proximalia dilata. Extrema raphium interna proximalia deflexa versus stigma. Striae latae, ad centrum (12–14/10 μm) parallelae, ad capitulum-polum (14–16/10 μm) dilute radiatae, basim-polum (13–14/10 μm) valde radiatae. Area porellibus apicalis bilobata distincta. Pseudosepta indistincta.*

*DESCRIPTION.* — Valves linear to lanceolate-cuneate, headpole narrow to rounded, footpole narrow. Length 18–27 μm. Breadth 3.5–5 μm. Axial area narrow at apices, expanded into a broad, oval central area. A single stigma is present. Raphe lateral, undulate, with dilated external proximal raphe ends, internal proximal raphe ends hooked towards stigma. Striae broad, parallel at the center (12–14/10 μm), slightly radiate at the headpole (14–16/10 μm), strongly radiate at the footpole (13–14/10 μm). Apical pore fields distinct. Pseudosepta not visible.

*HOLOTYPE.* — CAS 219037 (Fig. 26).

*TYPE LOCALITY.* — Surface of wet rocks, Cascade Ankitso, Madagascar.

*COMMENTS.* — *Gomphonema stigmatellum* is more linear in valve outline than *G. clevei* Fricke as shown in the original illustrations (in Fricke 1902, pl. 234) and in specimens from Africa (Gasse 1980; Kociolek and Stoermer 1991b). It is shorter in length than *G. christensenii* Lowe & Kociolek (1984), and also has a less expanded axial area.

**Gomphonema westii** Spaulding & Kociolek, sp. nov.  
(Figs. 29–33, 64–68)

*DESCRPTIO.* — *Valvae cuneatae, capitulo-polo late rotundato, basi-polo rotundato. Longitudo 24–30 μm. Latitudo 5.5–6 μm. Area axialis ad polos angusta expansa in aream centralem ovoideam. Stigma carens. Raphe undulata lateralis. Extrema raphium extra proximalia dilata. Extrema raphium interna proximalia deflexa lateraliter.*

*Area porellibus apicalis bilobata praesens. Lineae longitudinalis margines in latere alteruto areis axialis. Striae latae, ad centrum (10–12/10 μm) dilute radiatae dispositae magis late, ad capitulum-polum (13–14/10 μm) parallelae ad dilute radiatae, ad basim-polum (12–13/10 μm) radiatae. Pseudosepta distincta.*

*DESCRIPTION.* — Valves club-shaped, headpole broadly rounded. Footpole narrowly rounded. Length 24–30 μm. Breadth 5.5–6 μm. Axial area broad, ovoid at central area, narrowing at poles. Stigma absent. Raphe lateral, undulate, with external proximal raphe ends dilated, internal proximal raphe ends deflected laterally. A bilobed apical pore field is evident at the footpole. Striae broad and parallel at the valve center (10–12/10 μm), slightly radiate and becoming parallel at the headpole (13–14/10 μm), radiate at the footpole (12–13/10 μm). Striae crossed by longitudinal lines near the margin at both sides of the axial area. Pseudosepta evident.

*HOLOTYPE.* — CAS 219050 (Figs. 29, 30).

*ISOTYPE.* — BMNH West & West Collection (L666)

*TYPE LOCALITY.* — Lake Alastra, Madagascar.

*COMMENTS.* — *Gomphonema westii* differs from the other astigmatate *Gomphonema* from Madagascar in that the headpole is significantly expanded as compared to the footpole. The valves are robust and fairly heavily silicified. Longitudinal lines are less evident in this species and the axial plate is expanded almost to the valve margin.

**Gomphonema peracutum** Spaulding & Kociolek, sp. nov.  
(Figs. 34–38, 56–61)

*DESCRPTIO.* — *Valvae lineares, capitulo-polo et basi-polo rotundato. Longitudo 17.5–22 μm. Latitudo 3 μm. Area axialis ad polos angusta expansa in aream centralem ovoideam. Stigma carens. Raphe recta ad leviter undulata. Extrema raphium extra proximalia dilata. Extrema raphium interna proximalia deflexa lateraliter. Area porellibus apicalis bilobata distincta et basim-polum. Lineae longitudinalis positae prope margines in latere alteruto areis axialis. Striae ut videtur longior ad capitulum-polum quam basim-polum, ad centrum (13/10 μm) parallelae, ad capitulum-polum (15–16/10 μm) di-*

*lute radiatae*, *basim-polum* (13–16/10  $\mu\text{m}$ ) *valde radiatae*. *Pseudosepta evidentia ad polos*.

DESCRIPTION. — Valves nearly linear, headpole rounded, footpole narrowly rounded. Length 17.5–22  $\mu\text{m}$ . Breadth 3  $\mu\text{m}$ . Axial area narrow at the poles, expanded into an ovoid central area. Stigma lacking. Raphe straight to slightly undulate, with prominently dilated external proximal raphe ends. Internal proximal raphe ends laterally deflected. An apical pore field is evident at the footpole. Striae crossed by longitudinal lines positioned near the margin on both sides of the axial area. Striae appear longer at headpole than at footpole, parallel at center (13/10  $\mu\text{m}$ ), slightly radiate at headpole (15–16/10  $\mu\text{m}$ ), strongly radiate at the footpole (13–16/10  $\mu\text{m}$ ). Pseudosepta evident at both poles.

HOLOTYPE. — CAS 219036, (Fig. 35).

TYPE LOCALITY. — Surface of wet rocks, Cascade Ankitso, Madagascar.

In the SEM, puncta are lineolate externally and extend over valve margin and onto mantle (Fig. 56). Puncta at headpole are reduced in size (Fig. 56, 59). Between the axial area and margin, striae possess dark bands indicating the presence of an axial plate (Fig. 61). Externally, proximal raphe ends distinctly expanded (Figs. 56, 61). The raphe is narrow and indistinct (Figs. 56, 57). At the footpole, the raphe has a slight hook near the valve margin, and it extends over mantle in a straight line (Fig. 60). Apical pore fields are present, composed of simple porelli (Fig. 60). Internally, pseudosepta and helictoglossae are distinct. The central nodule is broad and rectangular, unilaterally expanded (Fig. 58), however proximal raphe ends were not visible.

COMMENTS. — *Gomphonema peracutum* is the smallest of the astigmatate Madagascar taxa described here. It differs from *G. apuncto* Wallace in having a more linear valve outline as well as possessing an axial plate (Kociolek and Kingston, submitted). Because of the small size of this species, longitudinal lines are less evident in LM (smaller axial plate) than in other taxa, but they remain a characteristic feature.

***Gomphonema quadratarea*** Spaulding & Kociolek, sp. nov.  
(Figs. 39–42, 62, 63)

DESCRIPTION. — *Valvae lineares cuneatae, capitulo-polo rotundato, basi-polo acuminato. Longitudo 16–21  $\mu\text{m}$ . Latitudo 3.2–3.5  $\mu\text{m}$ . Area axialis angusta linearis. Area centralis rectangularis ad ovalis dilute. Stigma carens. Raphe recta ad dilute lateralis. Extrema raphium extra proximalia dilata. Area porellibus apicalis bilobata distincta. Striae latae, ad centrum (14/10  $\mu\text{m}$ ) parallelae, ad capitulum-polum (16–18/10  $\mu\text{m}$ ) parallelae ad dilute radiatae, basim-polum (14–16/10  $\mu\text{m}$ ) dilute radiatae breves, plures late dispositae circum aream centalem. Pseudosepta indistincta ad polos.*

DESCRIPTION. — Valves linear, cuneate with headpole rounded, footpole acute. Length 16–21  $\mu\text{m}$ . Breadth 3.2–3.5  $\mu\text{m}$ . Axial area narrow, linear. Central area rectangular to slightly oval. Stigma lacking. Raphe straight, slightly lateral, with external proximal raphe ends dilated. Apical pore field distinct. Striae broad, parallel at the center (14/10  $\mu\text{m}$ ), parallel to slightly radiate at the headpole (16–18/10  $\mu\text{m}$ ), short, slightly radiate at the footpole (14–16/10  $\mu\text{m}$ ). Striae more widely spaced around the central area. Pseudosepta indistinct at both poles.

HOLOTYPE. — CAS 219036, (Fig. 40).

TYPE LOCALITY. — Surface of wet rocks, Cascade Ankitso, Madagascar.

In the SEM, puncta are lineolate externally (Figs. 62, 63) and located within wide foramina internally. Puncta at the headpole are reduced in size, and less elongate than other puncta (Fig. 63). Near the headpole the raphe has a slight deflection. Proximal raphe ends are distinctly expanded (Fig. 62) compared to the rest of the raphe (Fig. 63).

COMMENTS. — *Gomphonema quadratarea* differs from the other astigmatate *Gomphonema* from Madagascar in the distinct shape of the axial area. The axial area is narrow, forming a rectangular-like central area in contrast to the lanceolate and oval central area of the other taxa described here. The axial plate is reduced, the image of longitudinal lines in the LM is relatively close to the axis, in contrast to the longitudinal lines that appear midway to the valve margin in *G. perinsignis*.

#### DISCUSSION

Documentation of several new stigmatate and astigmatate *Gomphonema* species (Table 1) from



freshwaters of Madagascar indicates that the unique flora of this island-continent is reflected in the diatoms, as well as in the more well-known examples of terrestrial flora and fauna. Although the number of investigations relating to diatoms are few, a rich diatom flora of Madagascar is apparent (Manguin 1949a, 1949b, 1952; Spaulding and Kociolek, 1998). Manguin (1952) reported a unique diatom flora of the freshwater fossil deposits of Madagascar, describing 39 new forms or varieties and 18 new species. Others (Kociolek et al. 1997; Kociolek and Rhode 1998) established that *Actinella* taxa from Madagascar included 4 previously undescribed species.

Longitudinal lines are evident in light microscope images of several of the astigmatate Madagascar taxa. However, the structure of the axial plate responsible for the appearance of longitudinal lines differs from the structure of the axial plate of other gomphonemoid diatoms (i.e., members of the *Gomphoneis herculeana* group of Kociolek and Stoermer 1989, 1993). In the *G. herculeana* group, the axial plate extends perpendicular from the central sternum and a chamber is formed between the outer wall and the axial plate; the image of longitudinal lines is formed by the edge of the axial plate (Kociolek and Rosen 1984; Kociolek and Stoermer 1988). Other gomphonemoid diatoms may have a broad sheet of silica extending perpendicular from the axial area, but in these *Gomphonema* species no chambers are formed since the broad sheet of silica is solid. This gives the image of what has been termed in the literature as a "wide axial area" [present in taxa such as *G. manubrium* Fricke and *G. apuncto* Wallace (Kociolek and Kingston, submitted)]. In the Madagascar taxa, a suite of features is found that belong to both groups described above. As seen in the astigmatate Madagascar taxa, external slits along the axial area do not perforate the valve; a solid block of silica extends outward from the central sternum. This condition may exist for 1–2 or up to 5–6 slits within a striae away from the raphe branch before the slits perforate the valve. At this point the puncta are subtended by the siliceous lamina, and between the puncta and lamina exists a chamber. The edge of the lamina is responsible for the image of longitudinal lines in the light microscope.

Thus, observations on the Madagascar taxa imply a character state transformation series in-

volving the features of "wide axial area," "axial plate with partial chambers" (as seen in the Madagascar taxa) and "axial plate with entire chambers" (as seen in members of the *Gomphoneis herculeana* group), assuming the latter two features are indeed homologous. Given the disparity in geographic distribution of the two groups [Madagascar versus a "ring of fire" distribution plus a recent alien invasion of the *G. herculeana* group into continental Europe (Kociolek and Stoermer 1989; Coste and Ricard 1990)] the relationships of the two groups may not be close; this is indicated in the current analysis. Kociolek et al. (1997) showed that species within the genus *Actinella* from North America and Madagascar, though referred to the same species complex by Manguin (1949b), are not closely related. Thus, the two character states called "axial plate" may, in fact, not be homologous.

The number of astigmatate species of *Gomphonema* in Madagascar is remarkable. Grunow (in Van Heurck 1881) made the distinction between stigmatate (*Asymmetrica*, pl. 23–24) and astigmatate (*Symmetrica*, pl. 25) groups within *Gomphonema*, with only a small fraction of the total number of taxa lacking a stigma. Most of the previously described astigmatate *Gomphonema* species now belong to other genera. The number of astigmatate species in the genus is still relatively few (Table 2). *Gomphonema olivacea* and its close allies, as well as *G. transsilvanica*, are now considered within *Gomphoneis* (e.g., Kociolek and Stoermer 1989, 1993; Krammer and Lange-Bertalot 1985), and the genus *Gomphosphenia* was proposed for *G. grovei* and its allies (Lange-Bertalot 1995). Four new genera have been erected for the astigmatate, marine species formerly assigned to *Gomphonema* (Medlin and Round 1986). Further, Kociolek and Stoermer (1993) showed that the astigmatate *Gomphonema kaznakowi* Meresch-kowsky was not closely related to other typical *Gomphonema* species.

Astigmatate taxa from such geographic regions as South Africa (*G. rautenbachiae* Cholnoky, *G. crassestriatum* Fritsch and Rich) and South America (*G. demerarae* (Grunow) Frenguelli and *G. gibberum* Hustedt) have not been examined in SEM. Krammer and Lange-Bertalot (1985) provide illustrations of the astigmatate *G. brasiliense* Grunow (in Van Huerck 1881),

TABLE 2. Astigmatate *Gomphonema* taxa and their type locations.

Taxon	Type location
<i>Gomphonema abbreviatum</i> Agardh 1830	Europe
<i>G. apuncto</i> Wallace 1960	Southeast USA
<i>G. brasiliense</i> Grunow in Van Huerck 1878	Brazil
<i>G. christenseni</i> Lowe & Kociolek	Tennessee, USA
<i>G. crassestriatum</i> Fritsch & Rich 1924	South Africa
<i>G. demerarae</i> (Grunow) Frenguelli 1941	South America
<i>G. gibberum</i> Hustedt 1965	South America
<i>G. gomphopleuroides</i> Amosse 1969	Southeast Asia
<i>G. hasta</i> Skabitchevsky 1976	Siberia
<i>G. kaznakowi</i> Mereschkowsky 1906	China
<i>G. naviculoides</i> Skabitchevsky 1987	Siberia
<i>G. neobourrellyi</i> Moser et al. 1995	New Caledonia
<i>G. peruvianum</i> Grunow 1880	Peru
<i>G. puiggarianum</i> Grunow 1880	Brazil
<i>G. rautenbachiae</i> Cholnoky 1959	South Africa
<i>G. strictum</i> (Maillard) Lange-Bertalot & Moser 1995	New Caledonia

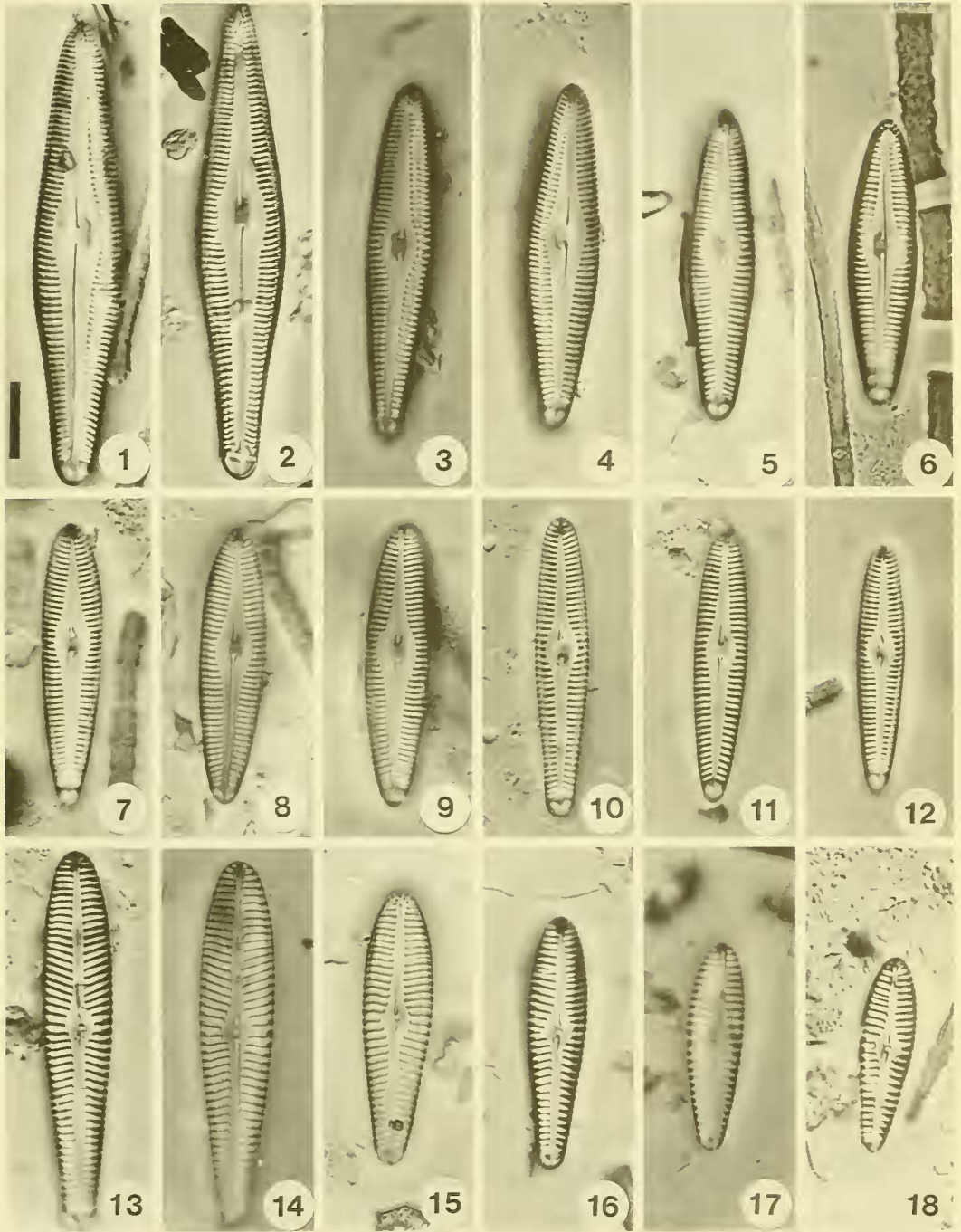
which appears similar (linear areolae, broad central area, unclear if illustration indicates an axial plate) to the astigmatate Madagascar taxa and should be further compared to the Madagascar group. The astigmatate *G. gomphopleuroides* Amossé (1969) described from Southeast Asia appears to share few features with *Gomphonema* sensu stricto. Astigmatate taxa [*G. neobourrellyi* Moser et al., *G. strictum* (Maillard) Lange-Bertalot and Moser] have been also reported from the tropics of New Caledonia (Moser et al. 1995). The narrow biogeographic ranges of these species from South America, Africa, and Asia may represent unique phylogenetic lineages distinct from (and perhaps only remotely related to) *Gomphonema*. The astigmatate condition in these diatoms may prove to be primitive, as has been suggested for *G. kaznakowi* (Kociolek and Stoermer 1993).

While some of the Madagascar taxa resemble South African taxa (*G. eurycephalus* compared to *G. latistigmata* and its allies, Passy et al. 1997), east African floras (Gasse 1980, 1986) show no clear affinity to the southern regions. Furthermore, *Gomphonema* species from Madagascar are distinct from those so far reported from the close, but isolated islands of Seychelles and Mauritius in the Indian Ocean (Coste and Ricard 1982a, 1982b). The diversity of closely related forms found in Madagascar is not surprising,

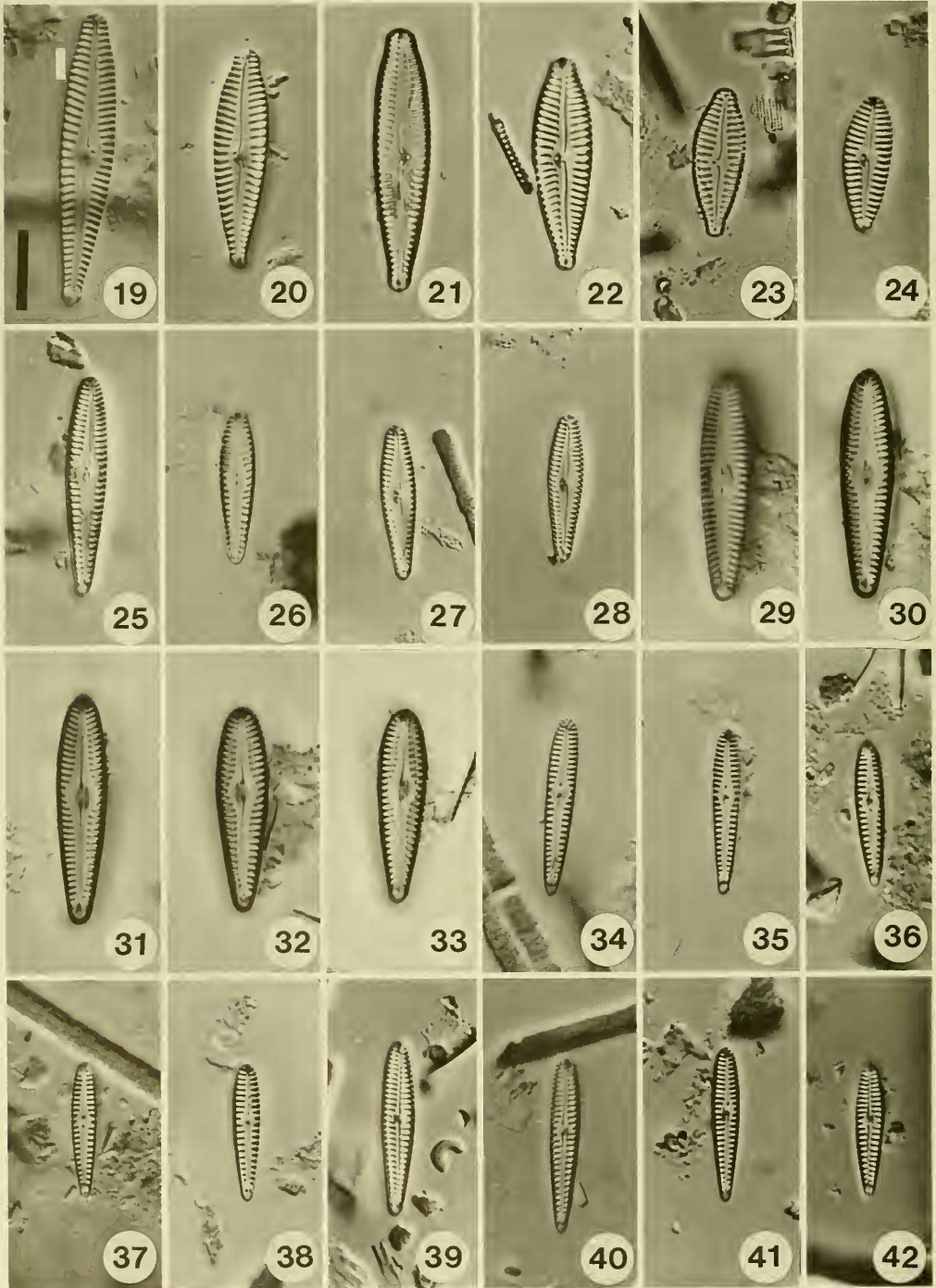
given that this island-continent has been isolated from Africa since the late Jurassic (140–160 MYA) (Barron et al. 1978). The rich endemic diatom flora of Madagascar, especially of astigmatate gomphonemoid forms, apparently form a distinct lineage within the freshwater gomphonemoid diatom lineage (Kociolek and Stoermer 1993). The gomphonemoid diatom flora is not only rich and endemic, but Madagascar taxa appear more closely related to one another than to taxa of geographic areas in near proximity. Similar results of endemism and geographic distribution were described in ancient rift lakes of East Africa (Kociolek and Stoermer 1993) and in Lake Baikal (Kociolek and Stoermer 1989).

#### ACKNOWLEDGMENTS

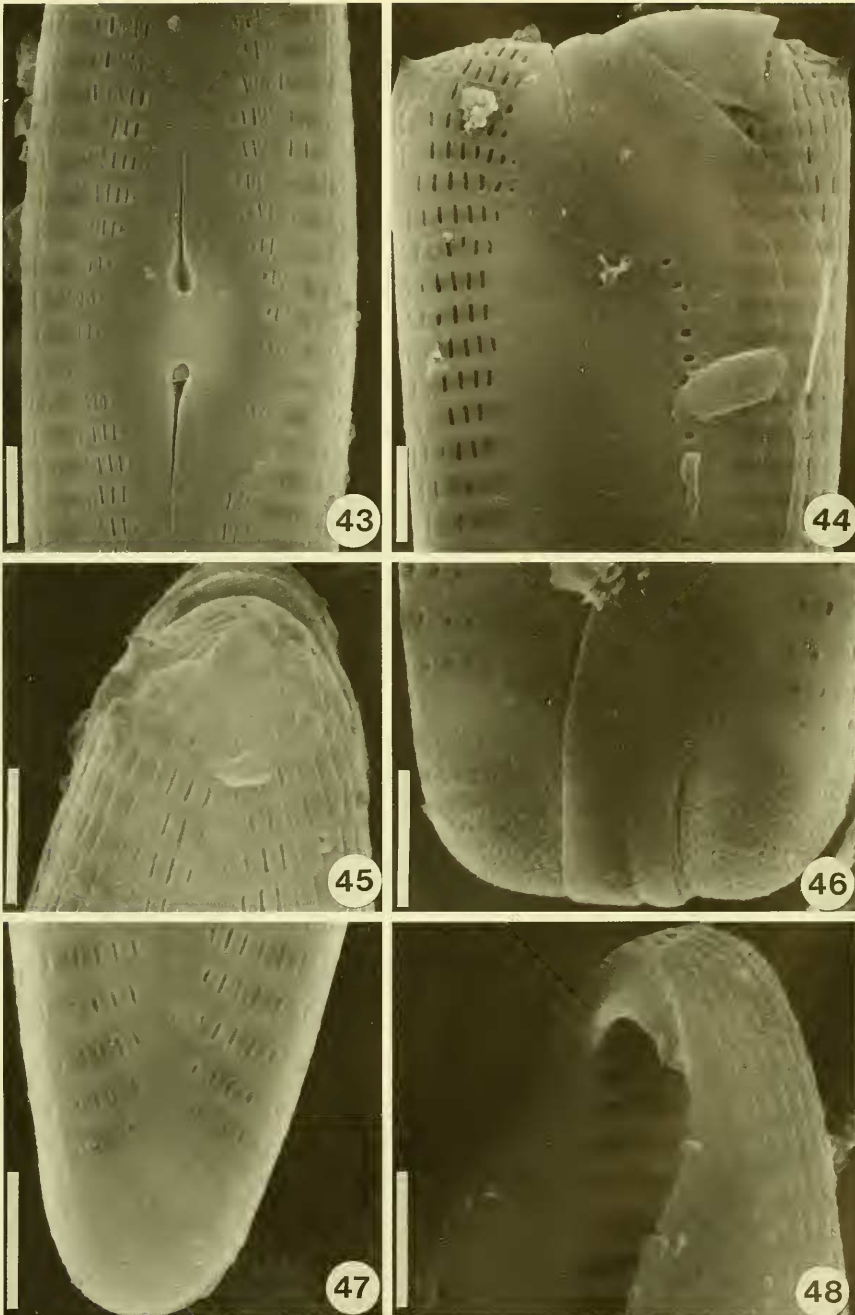
Bruno de Reviers (MNHN) and David M. Williams (BMNH) kindly provided loans of slides and material from original collections. We thank E. Fourtainer, K. Nutile and D. Wong for their contributions. Support for S. A. Spaulding was provided by a Postdoctoral Fellowship in the Diatom Collection of the Department of Invertebrate Zoology and Geology and J. P. Kociolek gratefully acknowledges support as a visiting professor at MNHN.



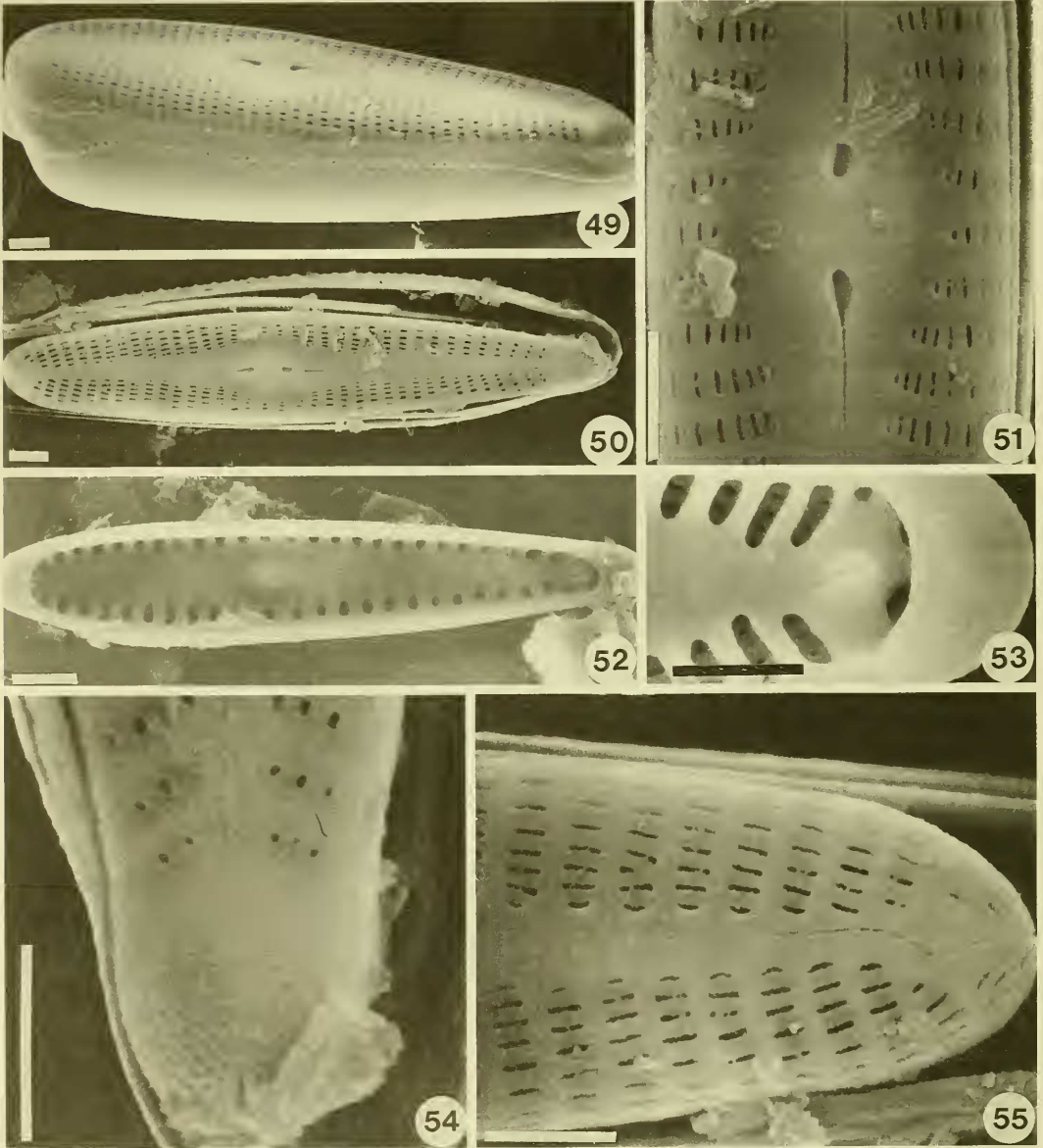
FIGURES 1-18. LM. FIGURES 1-6. *Gomphonema perinsignis*. FIGURE 3. Specimen from Manguin Collection (AD 8666), Antsirabe, Niv. 20 m. FIGURE 4. Holotype specimen, CAS 219037. FIGURES 7-9. *G. madagascarensis*. FIGURE 8. Holotype specimen, CAS 219036. FIGURES 10-12. *G. evanescens*, FIGURE 11. Holotype specimen, CAS 219036. FIGURES 13-18. *G. eurycephalus*. FIGURE 14. Holotype specimen, CAS 219037. Scale bar = 10  $\mu$ m.



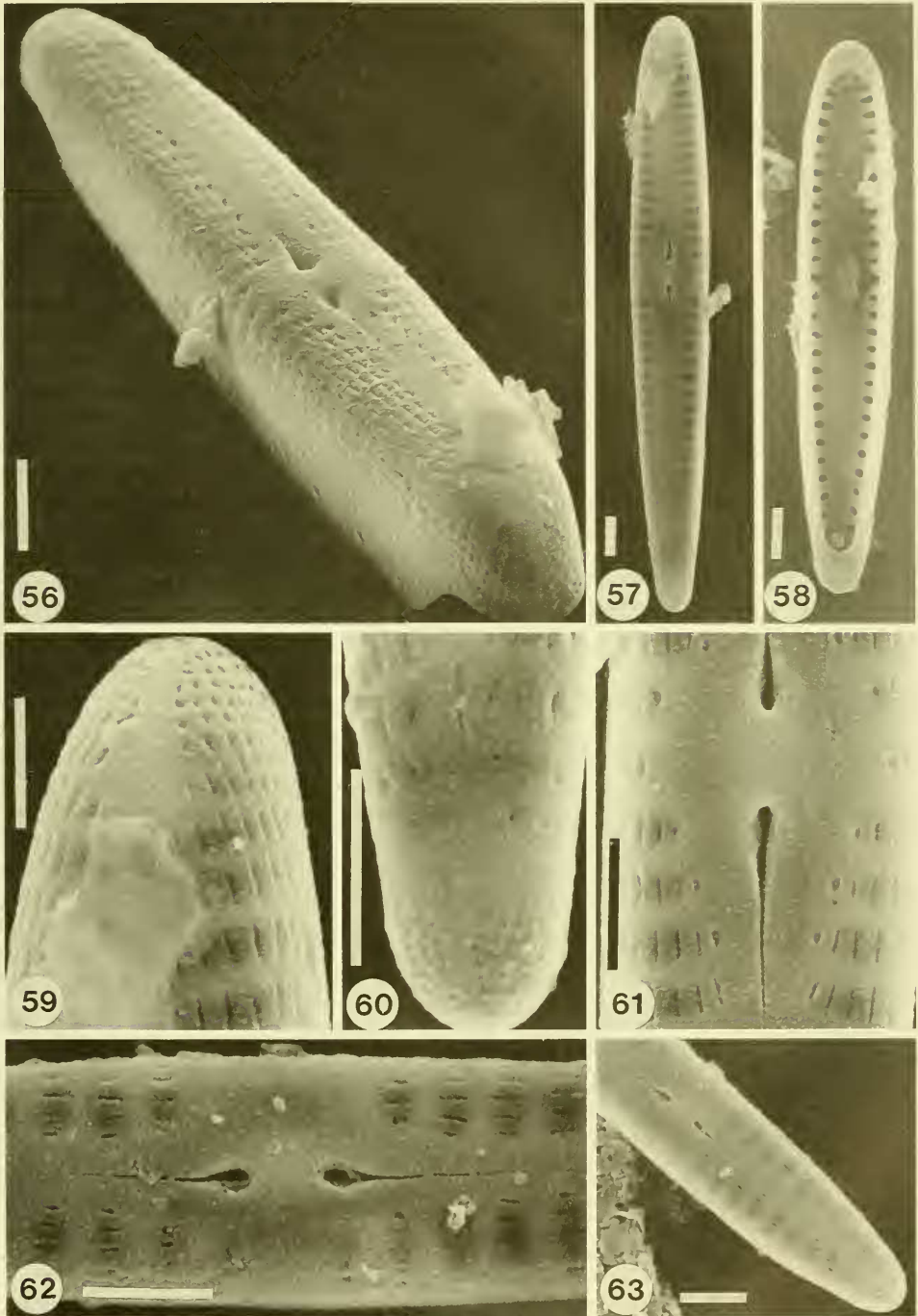
FIGURES 19–42. LM. FIGURES 19–24. *Gomphonema pulvillum*. FIGURE 19. Holotype specimen, CAS 219036. FIGURES 25–28. *G. stigmatellum*. FIGURE 26. Holotype specimen, CAS 219037. FIGURES 29–33. *G. westii*. FIGURES 29–30. Holotype specimen, CAS 219050. FIGURES 34–38. *G. peracutum*. FIGURE 35. Holotype specimen, CAS 219036. FIGURES 39–42. *G. quadratarea*. FIGURE 40. Holotype specimen, CAS 219036. Scale bar = 10  $\mu$ m.



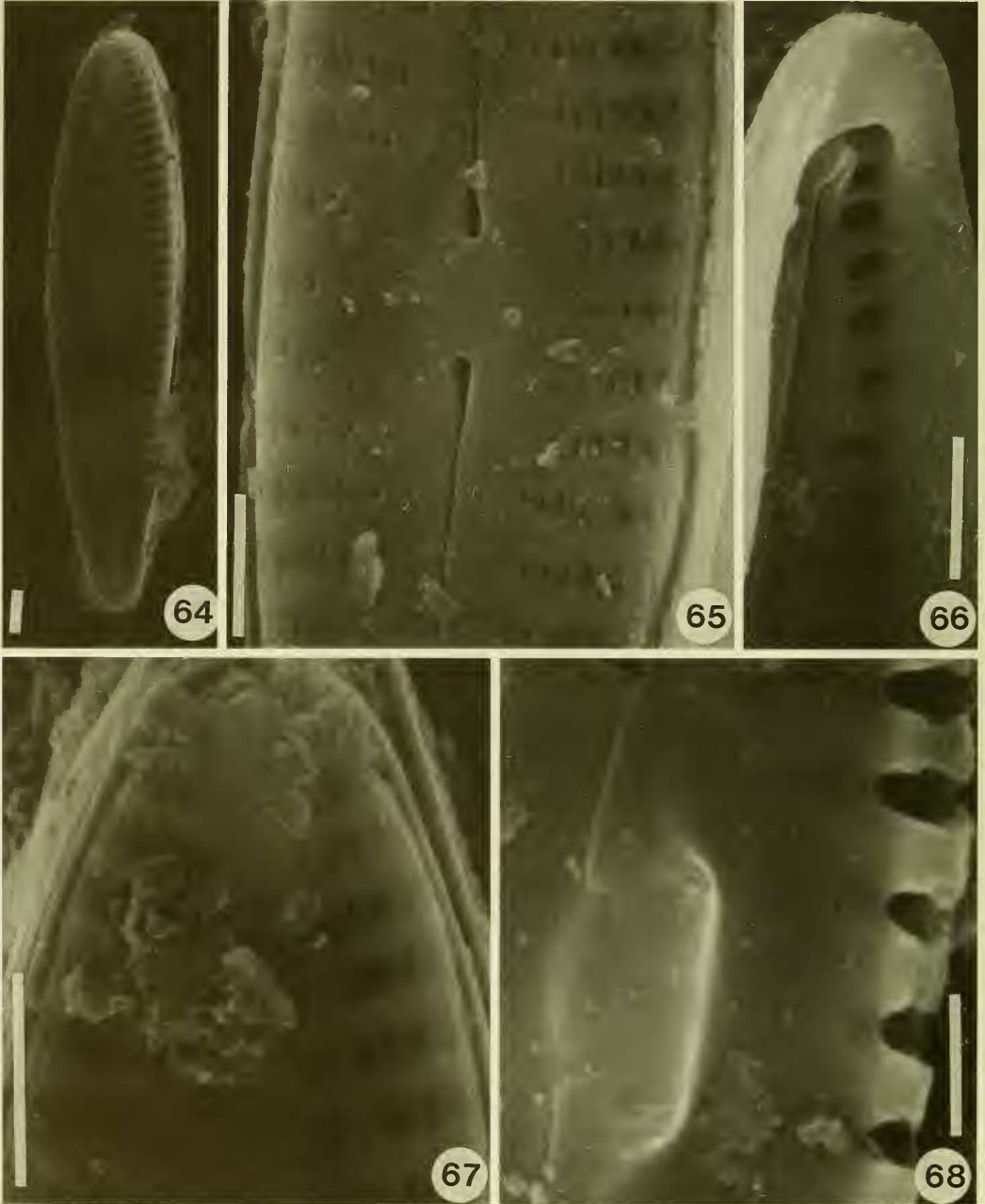
FIGURES 43–48. SEM, *Gomphonema perinsignis*. FIGURE 43. External view of central area with lineolate puncta that are occluded midway between the margin and central area by the axial plate. Dark bands indicate foramina open to the valve interior. Raphe is narrow and indistinct, becoming expanded and distinct proximally. FIGURE 44. Girdle view of headpole showing lineolate puncta on valve mantle. A small spine is present at the margin of valve apex. FIGURE 45. External view of headpole. Raphe has a slight bend and is slightly offset from the apical axis at the valve margin. FIGURE 46. Girdle view of footpole showing apical pore field. FIGURE 47. External view of footpole. Raphe has a slight hook near the valve margin. FIGURE 48. Headpole with partial internal view. Pseudoseptum and marginal lamina are evident. Scale bars = 2  $\mu$ m.



FIGURES 49–55. SEM, *Gomphonema evanescens*. FIGURE 49. External view of valve face and girdle. FIGURE 50. External view of valve face. FIGURE 51. External view of central area with lineolate puncta. Raphe is narrow and indistinct, becoming expanded and distinct proximally. FIGURE 52. Internal view of valve. Pseudosepta are present at each end. Axial plate and central nodule are evident. FIGURE 53. Internal view of footpole showing pseudoseptum and helictoglossa. Lineolate puncta are visible within foramina. FIGURE 54. External view of footpole. Raphe has a slight hook near the valve margin. FIGURE 55. External view of headpole. Raphe has a slight bend and offset from the apical axis at the valve margin. Scale bars = 2  $\mu$ m.

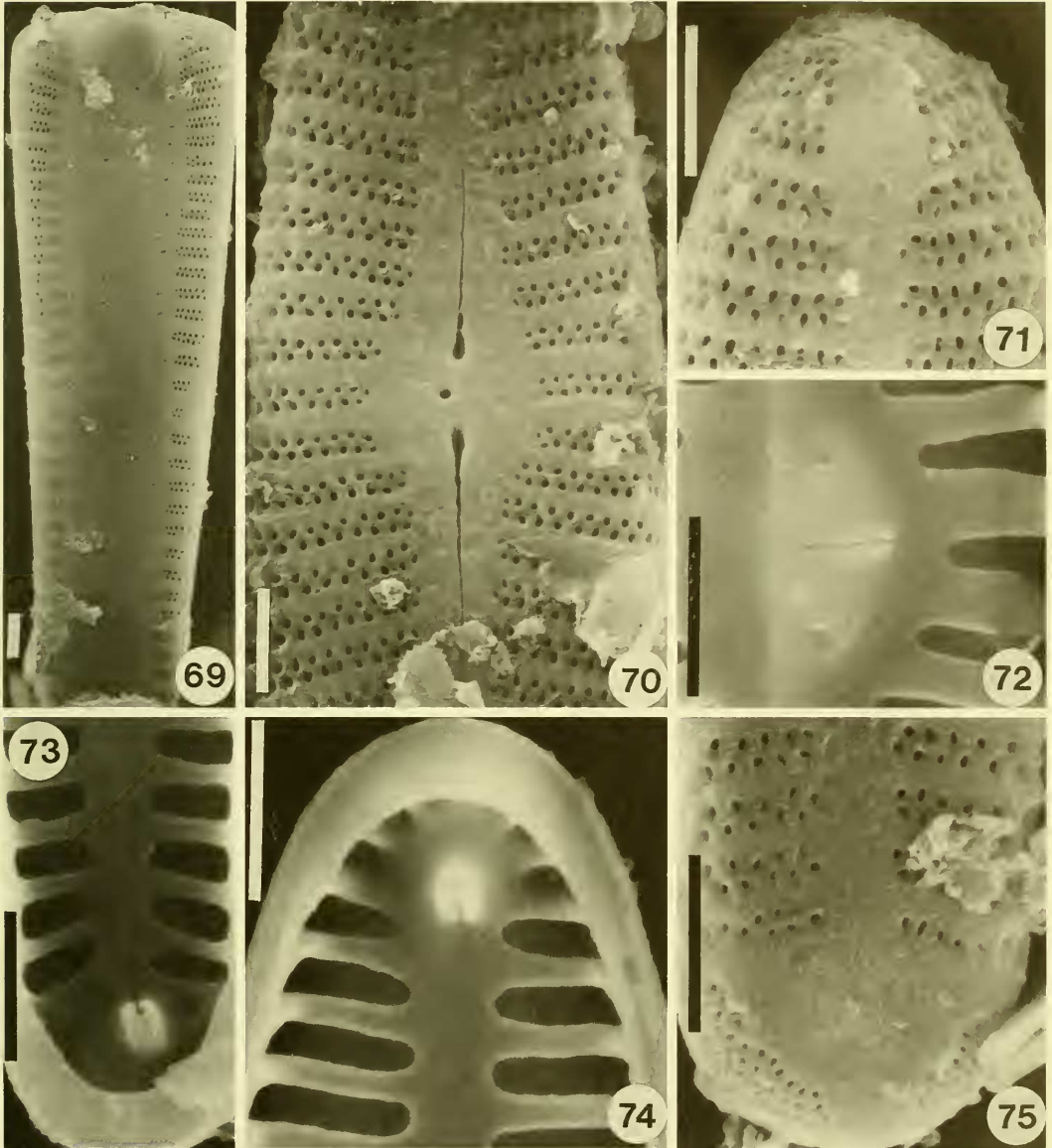


FIGURES 56–63. SEM, *Gomphonema peracutum* (FIGURES 56–61) and *G. quadratarea* (FIGURES 62–63). FIGURE 56. External view of valve. FIGURE 57. External view. Axial area narrow at the poles, expanded into an ovoid central area. FIGURE 58. Internal view of showing axial plate and central nodule. FIGURE 59. External view of headpole showing puncta at the headpole. FIGURE 60. External view of footpole with apical pore field. Scale bars = 2  $\mu$ m.



FIGURES 64–68. SEM, *Gomphonema westii*. FIGURE 64. External view of valve. FIGURE 65. External view of central area and lineolate puncta. FIGURE 66. Internal view of headpole showing pseudoseptum and helictoglossa. FIGURE 67. External view of headpole showing raphe with deflection near valve margin. FIGURE 68. Internal view of valve. Central nodule and proximal raphe terminus. Raphe is deflected toward central nodule and ends are recurved. Scale bar in FIGURE 68 = 1  $\mu$ m. Scale bars in remaining figures = 2  $\mu$ m.





FIGURES 69–75. SEM, *Gomphonema eurycephalus*. FIGURE 69. Girdle view of frustule and two copulae. Doubly punctate striae occur on valve mantle. FIGURE 70. External view of central area. Stigma is located centrally, in close proximity to proximal raphe ends. Puncta are circular to oval in shape and arranged in alternating rows. FIGURE 71. External view of headpole. FIGURE 72. Internal view of central nodule showing lateral deflection of proximal raphe ends and elongated (slit-like) internal expression of the stigma. FIGURE 73. Internal view of footpole. Helictoglossa and a small pseudoseptum is present. Puncta are located within foramina. FIGURE 74. Internal view of headpole showing helictoglossa and pseudoseptum. FIGURE 75. External view of footpole. Apical pore field is composed of circular porelli. Scale bars = 2  $\mu$ m.

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